

North-South Differentiation of Blennioid Fishes in the Central Pacific

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DIFFERENCES in the number of fin rays, scale rows, rings of bony armor (family Syngnathidae), and other meristic characters have long been employed as criteria for separating species and subspecies of fishes. With the recent increased interest in Central Pacific ichthyology numerous forms have been shown to exhibit minor differences in meristic characters between various geographical areas, and relatively extreme populations have been described as specifically or subspecifically distinct, depending upon the magnitude of the differences. The term *subspecies* has been a particularly popular one to apply to slightly divergent populations as it connotes both similarity and dissimilarity. In the Pacific, however, its use has been confusing from the standpoint of zoogeography, for often little or nothing has been said about gene interchange, effects of environmental factors, or method of distribution over vast expanses of ocean. For example, Herald (*in* Schultz *et al.*, 1953: 267, 273–275) distinguishes two subspecies of the pipefish *Corythoichthys flavofasciatus* on the basis of minor differences in meristic characters, and then says that the two forms are separated by a distance of 6,000 miles, with no other representatives of the species between them. A less extreme situation is Schultz's (*in* Schultz *et al.*, 1953: 292–297) erection of several subspecies of *Atherion elymus* based on slight differences in other meristic characters. In this case the forms occur in the Philippine, Marshall, and Mariana Islands, which are relatively close to-

gether compared to previous example, but considerable "island-hopping" must occur if there is interbreeding.

In the course of reviewing the blennioid fishes of the Hawaiian Islands the writer's attention has been drawn to a similar situation in that certain Hawaiian blennies bear a marked similarity to others from the Marshall Islands. The minimum distance between these two areas is about 1,400 miles, with practically no islands in between. Examination of specimens from Wake Island, one of the few intermediate geographical areas, indicated a rather surprising degree of intermediacy with respect to several morphological characters. Two hypotheses were formulated as a result of this discovery: 1) that there might be a traffic of fishes between the Marshalls and Hawaii by way of Wake, with a resultant possibility of gene interchange; and 2) that perhaps the intermediate nature of the Wake specimens was due to the intermediacy of some factor in the physical environment.

In considering the first hypothesis it is noteworthy that the prevailing ocean currents affecting the Hawaiian-Marshallese area act so as to move water from the Hawaiian Islands toward the Marshalls (Sverdrup *et al.*, 1946: chart 7). Consideration of this fact makes it obvious that if there is a movement of shore fishes between the Hawaiian and Marshall Islands it must normally be one-way, its point of origin being in Hawaii. If this is so then the high degree of endemism present in the Hawaiian shore fishes (reckoned as great as 52.6 per cent by Jordan and Evermann, 1905: 32) becomes a curious anomaly, as does

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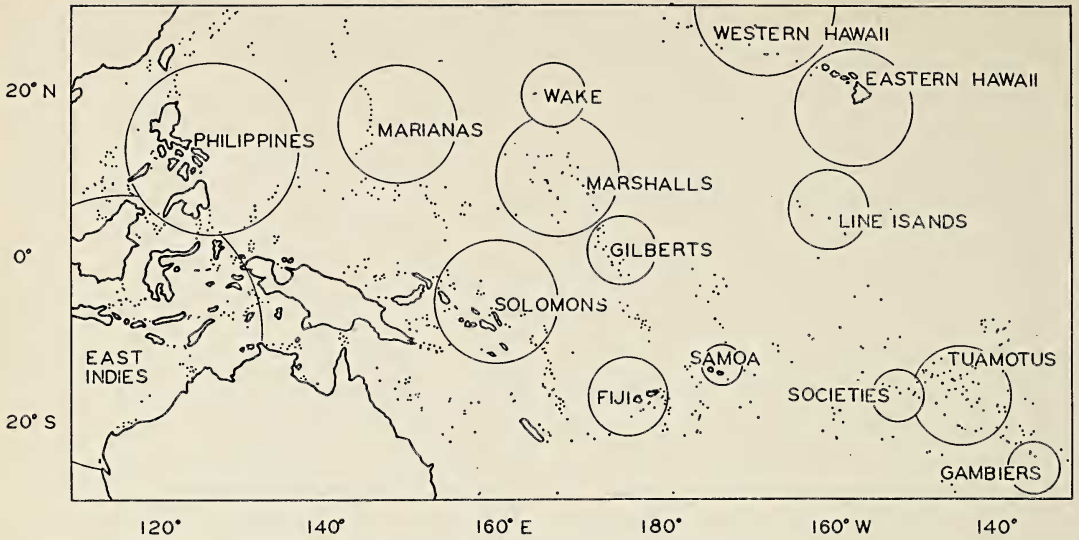


FIG. 1. Map showing relationships between various island groups of the Pacific Ocean. Circles denote areas from which specimens were examined.

the relatively distant relationship between the fishes of the Marshalls and Hawaii, as compared to the closer one between those of the Marshalls and the East Indies.

In order to investigate the second hypothesis the study was restricted to a single blenny, *Istiblennius edentulus*. This species is widely distributed throughout the Indo-Pacific region, but has evolved slightly different forms in certain isolated geographical areas. It, together with its close relatives, is a tidepool inhabitant and quite demersal in its habits. Spawning occurs in tidepools but the postlarvae are pelagic and are undoubtedly the stage in which dispersal of the species has occurred. Specimens from numerous island groups have been examined, and meristic data have been compared to an environmental condition, water temperature, in this work.

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GEOGRAPHIC AND PHYSICAL CONSIDERATIONS

The Central Pacific Ocean, using the term rather loosely, is crossed by a band of islands running in a general southeasterly direction from the Marianas to the Gambiers (Fig. 1). This strip is about 5,500 miles in length and covers approximately 50 degrees (3,000 miles) of latitude. Its component islands are quite regularly spaced across the Pacific, and thus form a convenient array for a study of the effects of latitude, and hence temperature, on fishes. Because of the possibility of fish movement between islands in this band, with resultant interbreeding and masking of temperature effects, it was deemed advisable to study specimens from various remote geographical areas. The following list summarizes collection locales for specimens examined; those regions marked with an asterisk do not lie on or particularly near the main band of islands.

- *Western Hawaii (Necker, Laysan)
- *Eastern Hawaii (Oahu, Maui, Hawaii)
- Wake
- Marianas (Guam, Saipan)
- *Philippines (Mindoro, Balabac)

Northern Marshalls (Bikini, Eniwetok,
Kwajalein, Rongelap)

Southern Marshalls (Arno)

*Line Islands (Fanning)

Gilberts (Onotoa)

*Solomons (Bougainville, New Georgia,
Nissan Group)

*East Indies (Java, Ste. Barbel)

Samoa (Apia, Tutuila)

Tuamotus (Fakarava, Makatea, Makemo,
Rangiroa)

Fiji

Societies (Tahiti, Hereheretue)

Gambiers (Mangareva)

Inasmuch as the above band of islands crosses the Equator it is obvious that as a general rule sea temperatures will be greatest near its center and least as the northern and southern extremes are approached. Factors acting to offset this theoretical distribution are ocean currents and the seasons, each of which is somewhat variable in itself. These two factors, together with limited data on hydrographical conditions, make computation of accurate temperature values quite difficult. In this work surface water temperatures have been taken from Sverdrup, *et al.* (1946: charts 2 and 3), and approximations of means computed by averaging the values given for February and August. These means are listed in Table 1, together with other data.

FAUNAL CONSIDERATIONS

Istiblennius edentulus was described by Bloch (*in* Bloch and Schneider, *Systema ichthyologiae*, p. 172, 1801) from Huaheine Island in the Societies. Chapman (*in* de Beaufort and Chapman, 1951: 331) records its distribution from various localities throughout the Pacific and Indian Oceans and the Red Sea. He also mentions (*loc. cit.*) that the forms of the species occurring in southern Japan, Hawaii, and the Marquesas are probably subspecifically distinct from the one occupying the rest of the distribution. The Japanese and Hawaiian forms have been described as full species, *Istiblennius enosimae* (Jordan and Snyder, U.

S. Nat. Mus., Proc. 25 (1293): 460, 1902), and *Istiblennius zebra* (Vaillant and Sauvage, *Rev. Mag. Zool.*, 3 (3): 281, 1875), while the Marquesan form is as yet undescribed. Marquesan specimens were not available for this study, and Japanese material was not used because of the difficulty of obtaining precise water temperatures from along the coasts of Japan.

Principal differences between *edentulus* and *zebra* are the number of fin rays, the development of the fleshy crest on the heads of females, the presence of a tiny cirrus on each side of the nape, and the extent to which females are covered with small dark spots. Chapman (*loc. cit.*) admits the inconsistency of the color pattern as a means of separating Indian Ocean *edentulus* from those of the East Indies, and in the writer's opinion this character also is not valid in the Central Pacific.

The presence or absence of nuchal cirri has been studied, and appears to be an excellent criterion for distinguishing the Hawaiian representative from the other forms of *edentulus*. Cirri are never present in *zebra* (based on 244 specimens), but are always present in the true *edentulus* except for an occasional (injured?) specimen lacking the cirrus on one side. Such a loss occurs randomly throughout the distribution of the species, and is not restricted to specimens from areas near the Hawaiian Islands as might be expected.

The relative size of the cephalic crest in females is possibly a character worthy of further consideration. This crest is most prominent in *zebra*, and examination of large numbers of this blenny revealed that crest area is related to fish size but also varies somewhat at random. Insufficient material was available to determine the precise relationship of crest area to water temperature.

MERISTIC DATA

Table 1 summarizes fin ray counts made on *edentulus* and its close relative, *zebra*, for various portions of their ranges. It also includes mean counts for soft rays and data on

TABLE 1
 COUNTS RECORDED FOR *Istiblennius edentulus* AND RELATIVES FROM THE PACIFIC OCEAN

LOCALE	NUMBER OF FIN RAYS													MEAN SURFACE TEMPERATURE (degrees C.)						
	Dorsal fin					Mean soft rays	Anal fin					Mean soft rays								
	XI	XII	XIII	XIV	19		20	21	22	23	20		21		22	23	24			
Western Hawaii*	5	56	1			22	36	4			21.71	62	3	46	13			22.16	24.2	
Eastern Hawaii*	1	171	10			1	28	134	19		21.94	182	1	4	112	64	1		22.33	24.8
Wake Island	1	17		1	8	9					20.44	18	3	9	6				22.17	26.2
Marianas		11		4	6	1					19.73	11	4	6	1				21.73	27.2
Philippines*	1	30	1	5	21	5	1				20.06	32	8	22	2				21.81	27.5
Northern Marshalls	1	20	1		20	2					20.09	22	4	16	2				21.91	27.2
Southern Marshalls	29	1	2	25	3						20.03	30	8	20	2				21.80	27.5
Line Islands*	2				2						20.00	2	1	1					21.50	26.2
Gilberts	3		1	1	1						20.00	3	1	2					21.67	28.0
Solomons*	11		2	8	1						19.91	11	3	8					21.73	28.0
East Indies*	4				3	1					20.25	4			4				22.00	28.0
Samoa	2	33	1	4	23	9					20.14	36	1	3	26	6			22.03	27.2
Tuamotus	5	1			4	2					20.33	6		4	2				22.33	26.2
Fiji	3				2	1					20.33	3		3					22.00	26.0
Societies	1	2			2	1					20.33	3	1	1	1				22.00	26.2
Gambiers	9	1			1	8	1				21.00	10		5	5				22.50	25.5

* Island groups not included in or near band of islands extending from Marianas to Tuamotus.

mean surface water temperature. These data have been arranged by latitude so that specimens from the northernmost islands (Western Hawaii) appear at the top, and those from the southernmost (Gambier Islands) at the bottom of the table. In counting, each fin ray with a separate and distinct base was listed as a single ray, and those rays split to a single base were also counted as one ray.

Inspection of Table 1 reveals a definite, but not absolutely regular, decrease in mean soft ray count as one goes from northern latitudes toward the Equator. Going south from the Equator the mean counts gradually increase, ultimately approaching or exceeding those found in the most northerly islands considered. Analysis of mean water temperatures shows that they follow the same general pattern.

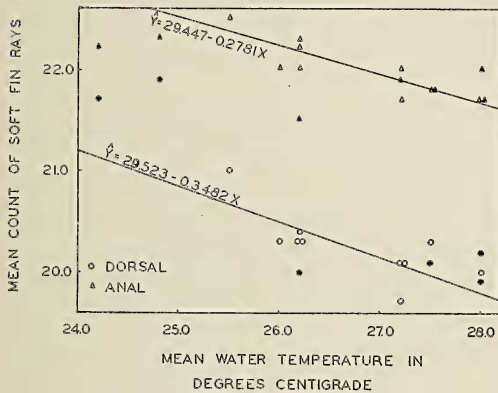


FIG. 2. Relationship between mean fin ray count and mean water temperature for *Istiblennius edentulus*. Hollow symbols represent data from main band of islands crossing Central Pacific (see text for details), solid symbols denote data from outlying islands. Regression lines calculated for main island band data only.

Figure 2 depicts the relationship between mean ray counts and mean water temperature, all figures here being rounded to one decimal place. Regression equations have been calculated for data from the main island band (excluding Western and Eastern Hawaii, the Philippines, the Line Islands, the Solomons, and the East Indies), and are as follows:

$\hat{Y} = 29.523 - 0.3482X$ for the dorsal fin, and $\hat{Y} = 29.447 - 0.2781X$ for the anal fin. Since these two lines are approximately parallel it may be inferred that temperature has about the same effect on each fin.

It is noteworthy that certain of the points (solid symbols on Fig. 2) representing data from areas not on the main island band occur at considerable distances from the regression lines. Fiducial limits have been set for expected ray counts at various temperatures along the regression lines, using the formula $S_{\hat{Y}} = s_{yx} \sqrt{1/n + x^2/Sx^2}$ (Snedecor, 1946: 120) and values of t at the $p_{.01}$ level. These limits together with the actual ray counts are presented in Table 2.

From Table 2 it is apparent that fin ray counts of populations from various remote areas differ significantly from the values expected on the assumption of a linear relationship between ray counts and temperature. It is equally apparent that specimens from other remote areas have counts which are well in line with the expected figures. In the former category is Eastern Hawaii (dorsal rays), with Western Hawaii (anal rays) and the East Indies (dorsal and anal rays) being borderline cases. The Line Island data are based on only two specimens, and while their ray counts are significantly different from the expected values, the small sample size precludes emphasizing them.

DISCUSSION

It has been shown in Figure 2 that a close relationship exists between water temperature and fin ray count for *I. edentulus*. While the specimens upon which this conclusion is based came from a long chain of closely spaced islands it was also apparent (Table 2) that specimens from certain remote islands fitted quite well into this general picture. The Eastern Hawaiian Islands apparently represent a geographical region where other factors, presumably mutation, have offset the mean ray count from the expected values. Western

TABLE 2
ACTUAL MEAN RAY COUNTS AND EXPECTED RANGE IN MEAN RAY COUNTS FOR *Istiblennius edentulus*
AND RELATIVES FROM OUTLYING ISLANDS

ISLAND	DORSAL FIN		ANAL FIN	
	Actual count	Expected range	Actual count	Expected range
Western Hawaii.....	21.7	20.3-21.9	22.2	22.2-23.2
Eastern Hawaii.....	21.9	20.3-21.5	22.3	22.1-23.0
Philippines.....	20.1	19.6-20.3	21.8	21.6-22.0
Line Islands.....	20.0	20.1-20.7	21.5	22.0-22.3
Solomons.....	19.9	19.3-20.2	21.7	21.4-22.0
East Indies.....	20.2	19.3-20.2	22.0	21.4-22.0

Hawaii and the East Indies are borderline instances of the same phenomenon, with the Line Islands possibly being so.

Several questions may be asked in connection with the above statements, probably the most important having to do with the validity of the supposed relationship between mean *annual* water temperature and the short period in ontogeny in which the number of fin rays is determined. Clearly this presumption can lead to certain errors, particularly in the case of fishes living in tidepools, the temperature of which is notoriously variable. Until further information is forthcoming on the embryology of Central Pacific fishes, however, mean temperature data must be used in working with museum specimens. Annual data are perhaps best since they average seasonal vicissitudes.

A second question which arises has to do with the taxonomic categories to be employed when dealing with a form showing meristic differences between various island groups. Obviously, if populations from areas representing extreme temperatures are considered they could be regarded as subspecifically distinct. When data are obtained from a more or less continuous series of islands, such as the band running from the Marianas to the Gambiers, however, it becomes apparent that extreme populations may be united by an evenly graded series. It is possible that specimens from an island in such a band are

essentially ecotypes (as used by Dice, 1952: 397), but because of our lack of knowledge regarding the inheritance and adaptive significance of fin ray number this must be left as theory at present. It seems more credible that populations from a given locale actually represent ecophenes, that is, the precise number of their fin rays is affected by some environmental factor such as temperature. In their discussion of the response of ecophenes to their environment neither Dice (1952: 399) nor Allee *et al.* (1949: 626) mentions the heritability or adaptational value of the change wrought by the response, and in light of Tåning's experimental work (1944, 1952) it may probably be assumed that neither factor is involved in the case of *I. edentulus*. If populations within the major distribution of *edentulus* actually represent ecophenes then it would be superfluous to label them with any taxonomic category below the species.

A third question has to do with the possible presence of mutations affecting the number of fin rays. It may be argued that the clinal distribution of ray counts seen in Table 1 could be produced by the gradual spread of such mutations. If this were so then a mutation acting to decrease the number of fin rays would have to occur near the Equator in order to account for the symmetrical distribution of ray counts on either side of that region. Furthermore, it would also have to occur in the Philippines and the Solomons to account

for the low number of fin rays there. If the mutation acted to increase fin ray number then it would need to appear at both the northern and southern limits of the band of islands, again to explain the symmetry seen in Table 1. Because of the unlikelihood of these occurrences, as contrasted with the much more plausible temperature effects, mutation may probably be ruled out from the fin ray picture seen in the islands extending from the Marianas to the Gambiers.

It is very likely that *I. zebra*, the Hawaiian form of *edentulus*, was derived from a stock of *edentulus*-like blennies which acquired a high number of fin rays because of the temperature effects here discussed. Because of geographical isolation and mutation it subsequently evolved into its present form. Its lack of nuchal cirri, possession of a well-developed cephalic crest in females, and distinctive fin ray counts probably warrant its consideration as a full species.

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